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Pilocosta (Melastomataceae) Revisited: A New Species, Polyploidy, and the Base Chromosome Number of the Genus

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ABSTRACT. A synoptic review of *Pilocosta* is presented to facilitate identification and comparison of a new species, *P. nubicola*, which is described and illustrated. An original chromosome count of $n = 11$ is reported for this species, together with updated geographic and taxonomic notes and a revised key to the five known species in the genus. Based on an evaluation of recorded chromosome counts, $x = 11$ is established as the base chromosome number of *Pilocosta*.

Pilocosta, one of about 25 genera in the traditionally recognized tribe Tibouchineae, is characterized by its quadrate hypanthia and four-merous flowers that are solitary, axillary, and ebracteate.

In the paper proposing *Pilocosta* as a new genus, Almeda & Whiffin (1981: 310) emphasized the distinctiveness of two collections from Costa Rica's Cordillera de Tilarán that appeared to be related to *P. erythrophylla*. My subsequent fieldwork has yielded additional material of this rare and little-collected *Pilocosta*. Analysis of this material and a study of meiotic chromosomes now provide compelling evidence for formal recognition of this entity as a new species described here as *P. nubicola*. To facilitate identification and comparison, it is presented in the context of a brief synopsis with a revised key to the five known species of *Pilocosta*, a discussion of the base chromosome number of the genus, and updated taxonomic and geographic notes.

The Base Chromosome Number of *Pilocosta*

The gametic chromosome number is reported here for *P. nubicola*. Meiosis was regular with 11 bivalents at diakinesis in all cells examined (Fig. 1A, B). Bud material for this count was collected from a natural population in the field, fixed in modified Carnoy's (Bradley, 1948) solution (4 chloroform, 3 ethanol, 1 glacial acetic acid, v/v/v/), and stored under refrigeration. Counts were made using a Zeiss light microscope with phase contrast and a 100× oil immersion objective. Drawings of meiotic figures were made with camera lucida at a magnification of 2100×. The type collection is the voucher for this count.

With this report, chromosome numbers are now known for all described species of *Pilocosta*. A count of $n = 11$ for *P. nubicola* is in agreement with records for *P. campanensis* (Almeda, 1989) and a Panamanian population of *P. oerstedii* (Almeda & Chuang, unpublished). It is now clear that *P. nana*, with populations having $n = 22$ (Almeda & Chuang, unpublished) and $n = 33$ (Almeda & Whiffin, 1981), consists of tetraploid and hexaploid races, respectively, based on $x = 11$. The occurrence of $n = 11$ or multiples of this number in four of the five species of *Pilocosta* leaves no doubt that $x = 11$ is the basic chromosome number in the genus. Both $n = 7$ and $n = 14$ were reported for *P. erythrophylla* (Almeda & Whiffin, 1981). We can now disregard $n = 7$ as a possible base number in *Pilocosta*. Of the more than 420 species of Melastomataceae for which chromosome counts are available, only 13 have numbers lower than $n = 9$. These lower numbers occur in a diverse assemblage of specialized species, which suggests that they have been derived from an ancestral diploid taxon by descending dysploidy.

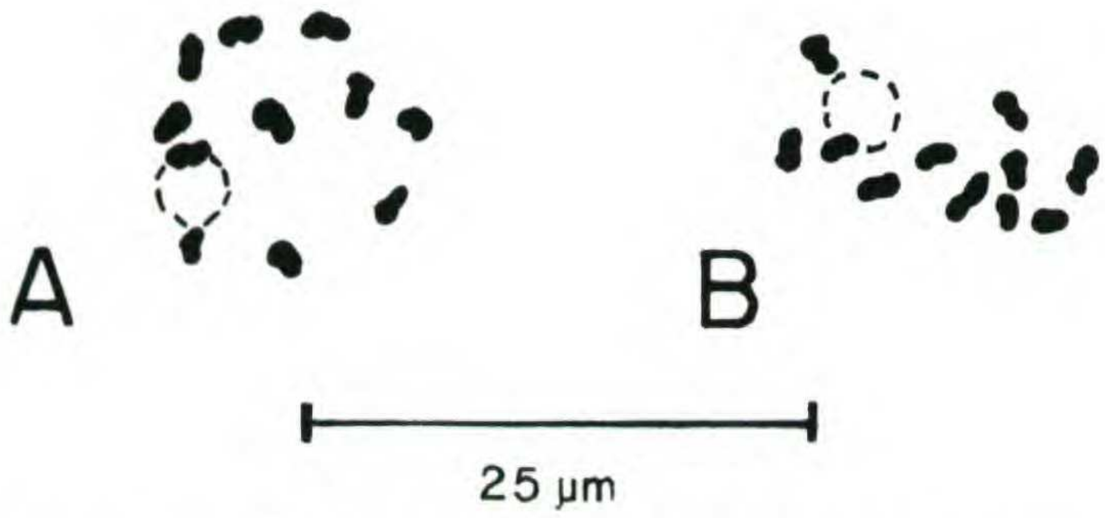


Figure 1. Camera lucida drawing of meiotic chromosome figures. —A, B. *Pilocosta nubicola*, $n = 11$, diakinesis (*Almeda & Daniel 7065*).

A chromosome count of $n = 18$ for two Costa Rican populations of *Pilocosta oerstedii* (Almeda & Whiffin, 1981) is the most enigmatic report to date because a single count from a Panamanian population is $n = 11$. It is tempting to speculate that $n = 18$ may have originated as a dysploid derivative of an ancestral tetraploid population with $n = 22$. Alternatively, dysploid reduction from $n = 11$ to $n = 9$, followed by polyploid gain, would also account for the origin of $n = 18$.

With haploid chromosome numbers of $n = 7$, 11, 14, 18, 22, and 33, *Pilocosta* is remarkably diverse for a genus of its size. Chromosome information has been a helpful source of data in circumscribing species. It is also useful in corroborating the generic distinctiveness of *Pilocosta*. *Tibouchina*, the genus to which described species of *Pilocosta* were assigned prior to 1981, is characterized by $x = 9$ (Almeda & Chuang, 1992). Although no species of *Pilocosta* has $n = 9$, the suggestion that this be considered a prime number in any attempt to make phylogenetic inferences in the genus (Almeda & Whiffin, 1981) is now untenable. This hypothesis was based on the observed frequency of $x = 9$ in genera of Tibouchineae then known cytologically and the report of $n = 18$ for *P. oerstedii*.

Almeda & Whiffin (1981) also commented on the intraspecific polyploidy in *P. erythrophylla*, noting that differences in ploidal levels could not be correlated with morphological, ecological, or geographical differences. This observation can now be extended to the polyploid races of *P. nana* and may also apply to *P. oerstedii*.

Although two species of *Pilocosta* have retained the base chromosome number of 11, polyploidy and dysploidy clearly have played a role in cytoevolution of the other three species. In the species of *Pilocosta* with more than one cytotype, a pattern emerges in which chromosomal evolution is evidently promoting reproductive isolation but preceding any significant morphological differentiation.

KEY TO THE SPECIES OF *PILOCOSTA*

1a. Principal leaves 12–40(–48) mm long, sparsely to copiously pubescent on both surfaces, innermost pair of lateral primary veins diverging from the midvein (1–)1.5–8 mm above blade base; calyx lobes on fruiting hypanthia 3–7 mm long (excluding apical setae).
  2a. Plants distinctly woody; stamens differing markedly in posture, size, and coloration, stamens of the larger (antesepalous) whorl geniculate at the filament insertion, connective prolonged 1.5–3 mm below anther thecae.
    3a. Hypanthia densely pilose to sericeous on the four prominent angles, otherwise glabrous, the trichomes soft, smooth, and silky to touch; Costa Rica and western Panama .... 5. *P. oerstedii*
    3b. Hypanthia moderately setulose on and between the four prominent angles, the trichomes rigid, minutely barbed or roughened apically and bristly to touch; central Panama ..... 1. *P. campanensis*
  2b. Plants herbaceous; stamens differing somewhat in size but similar in posture and coloration, stamens of the larger (antesepalous) whorl ± erect or ascending but not strongly geniculate at the filament insertion, connective prolonged 0.25–0.5 mm below anther thecae.
    4a. Abaxial foliar surface and hypanthium uniformly red in color; fruiting hypanthium 7–8 mm long on pedicels 5–9 mm long, pubescent only on the four prominent angles ... 4. *P. nubicola*
    4b. Abaxial foliar surface and hypanthium typically green (occasional individuals have some leaves with an irregular flush of pigmentation); fruiting hypanthium 9–13 mm long on pedicels (6–)9–20 mm long, pubescent on and between the four prominent angles ..... 3. *P. nana*
1b. Principal leaves 2–13 mm long, moderately to densely pubescent on the upper (adaxial) surface but essentially glabrous on the lower (abaxial) surface or with scattered trichomes largely restricted to the elevated primary veins, innermost pair of lateral primary veins diverging from the midvein 0.5–1 mm above blade base; calyx lobes on fruiting hypanthia 1–3 mm long (excluding apical setae) ..... 2. *P. erythrophylla*

SYNOPSIS OF *PILOCOSTA*

1. Pilocosta campanensis (Almeda & Whiffin) Almeda, Proc. Calif. Acad. Sci. 46: 219. 1989. Basionym: *Pilocosta oerstedii* (Triana) Almeda & Whiffin subsp. *campanensis* Almeda & Whiffin, Syst. Bot. 5: 306. 1980 [1981]. TYPE: Panama. Panamá: Cerro Campana, 10 Dec. 1967, *Lewis et al. 3069* (holotype, MO; isotypes, COL, DUKE, F, K, NY, UC).

This species is endemic to west-central Panama where it occurs in the provinces of Coclé, Herrera, and Panamá at 300–1,100 m. In habit and androecial morphology *Pilocosta campanensis* is most similar to *P. oerstedii*. These two species displace one another geographically, with *P. campanensis* typically occurring in wetter sites and at lower elevations.

2. Pilocosta erythrophylla (Gleason) Almeda & Whiffin, Syst. Bot. 5: 309. 1980 [1981]. Basionym: *Tibouchina erythrophylla* Gleason, Phytologia 1: 133. 1935. TYPE: Costa Rica. Heredia: Yerba Buena, Feb. 1926, *Standley & Valerio 49048* (holotype, US; photograph, NY).

This species appears to be restricted to perpetually wet habitats. It occurs in a relatively small area of Costa Rica's Cordillera Central on the slopes and valleys between Volcán Barva and Cerro Zurquí, extending to the lower western slopes of Volcán Irazú at 1,480–2,000 m.

Within its limited range, *P. erythrophylla* has populations with $n = 7$ and $n = 14$. A more extensive series of counts is needed to determine whether diploids outnumber the tetraploids or vice versa. This species is somewhat variable in internode length and leaf size, but pollen samples for plants from both chromosomal races have a mean diameter of 15.9 μm.

3. Pilocosta nana (Standley) Almeda & Whiffin, Syst. Bot. 5: 307. 1980 [1981]. Basionym: *Chaetolepis nana* Standley, Field Mus. Nat. Hist., Bot. Ser. 4: 247. 1929. TYPE: Panama. Bocas del Toro: region of Almirante, Jan.–Mar. 1928, *Cooper 233* (holotype, F; photograph, NY).

Pilocosta nana has the most widespread geographic and elevational range of any species in the genus. It is known from Volcán Arenal in north-central Costa Rica south to the Cordillera Central extending disjunctly to western and central Panama, northern Colombia (Magdalena), and northern Ecuador (Pichincha) at 450–2,000 m. The single collection from Ecuador was made in 1984 at 800 m (*Betancourt 119*, US).

This is the only species that occasionally grows sympatrically with other congeners. I have found it growing with *P. erythrophylla* in Costa Rica and with *P. campanensis* and *P. oerstedii* in Panama. The differing chromosome numbers between *Pilocosta nana* and each of the above-mentioned taxa probably account for the lack of intergradation where they grow together.

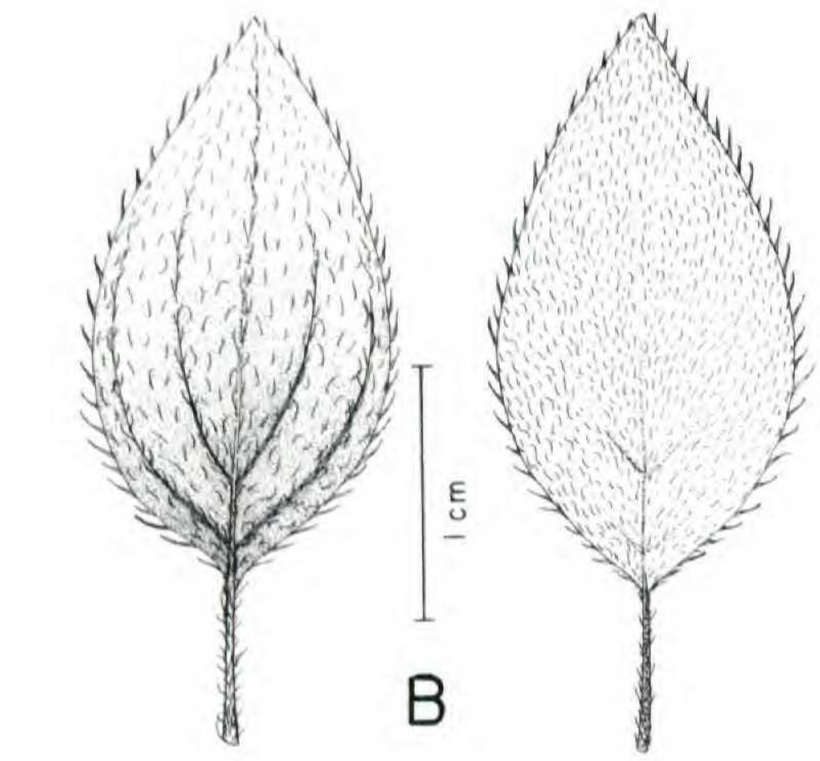
Pilocosta nana is also the most variable species in the genus. Chromosome counts for most populations analyzed to date are hexaploid with $n = 33$, but one tetraploid population with $n = 22$ has recently been collected in the Cerro Colorado region of western Panama. The different ploidal levels of *P. nana* are indistinguishable morphologically except that there appears to be a tendency for the tetraploid to have hypanthia that are more sparsely pubescent to glabrate between the four angles.

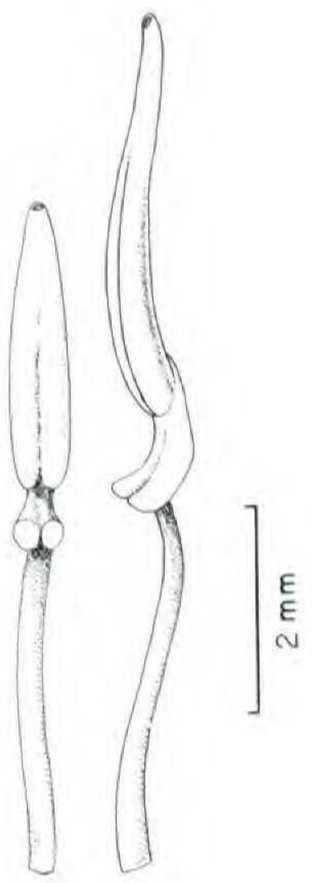
In terms of leaf size, hypanthial length, and pollen diameter (mean 27.8 μm; range 25.9–30.5 μm), *P. nana* exhibits the classic "gigas" syndrome associated with the polyploid condition. Its comparatively broad geographic and elevational range also lends support to the postulate that chromosome doubling may propel a population into a new adaptive sphere, rendering it capable of occupying habitats beyond the limits of its diploid progenitor (Levin, 1983; Lewis, 1980).

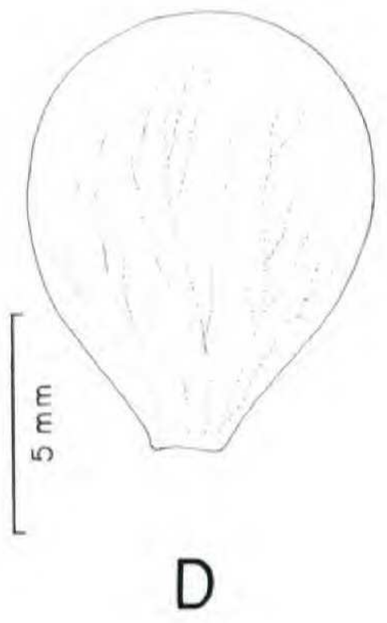
4. Pilocosta nubicola Almeda, sp. nov. TYPE: Costa Rica. Alajuela: Cordillera de Tilarán, Monteverde Cloud Forest Reserve, continuation of El Camino into the Peñas Blancas valley, 25 Feb. 1992 (fl, fr), *Almeda & Daniel 7065* (holotype, CAS; isotypes, CR, MO, US). Figure 2.

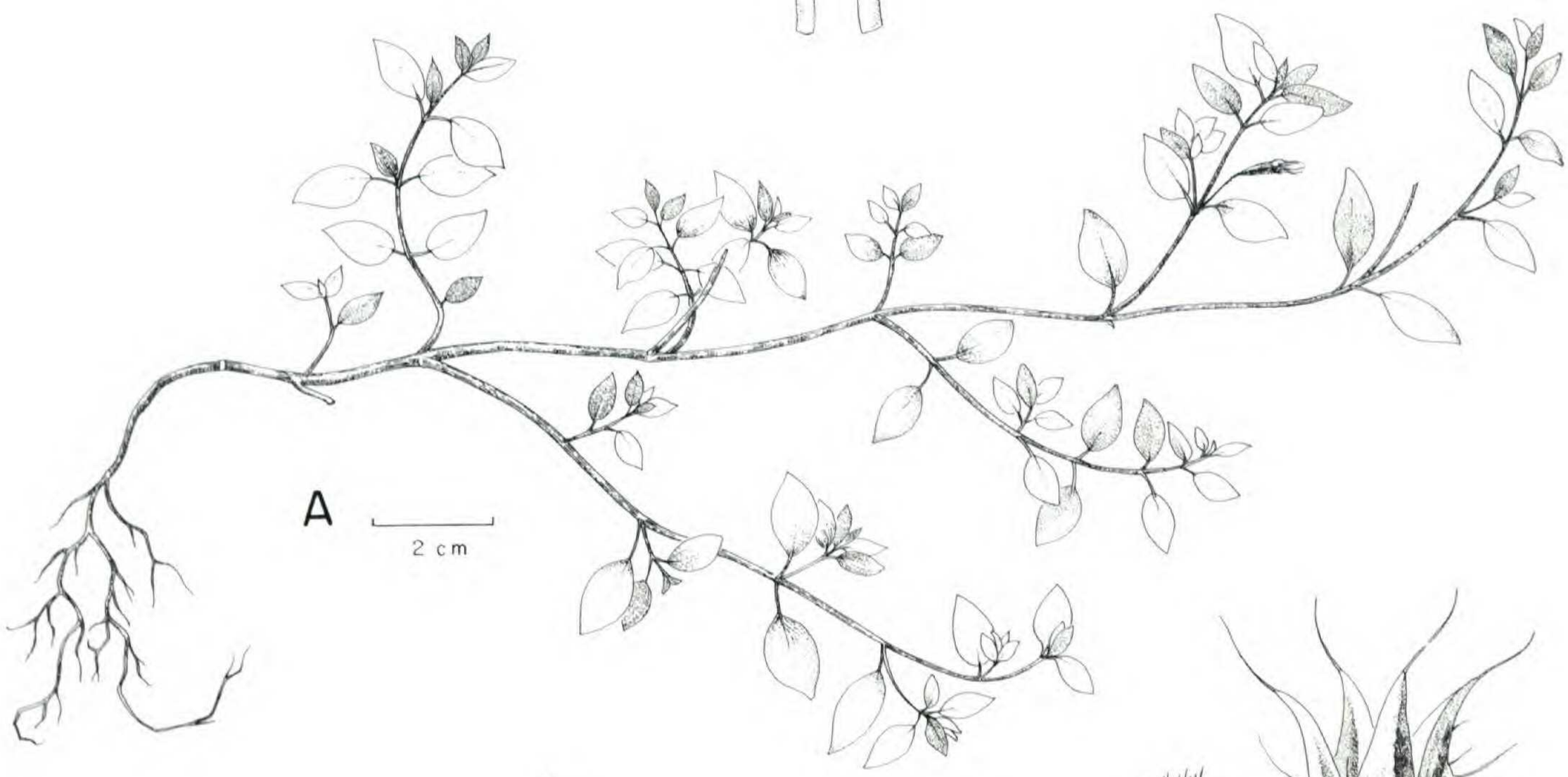
Herbae perennes, caules diffusi prostrati ramosi gracillimi, 4-angulati, demum subteretes, ad angulos sparse vel modice pubescentes pilis curvato-adscendentibus. Petioli 2–7 mm longi; lamina 12–26 × 8–18 mm ovata vel elliptico-ovata, apice acuta basi obtusa vel rotundata, supra dense vel modice albo-villosa, subtus rubra, sparse vel modice strigosa, 5–7-plinervata. Flores 4-meri, pedicellati et ebracteati in foliorum superiorum axillus solitarii. Hypanthium (ad torum) 7–8 × 2.5 mm, quadrangulare et manifeste 4-costatum, inter angulos glabrum et ad angulos sparse vel modice pubescens pilis curvato-adscendentibus; calycis lobi 3 × 2 mm anguste oblongo-triangulares persistentes. Stamina dimorphica; antherarum thecae subulatae apice uniporoso poro ventraliter inclinato. Connectivo ad basim 0.25 vel 0.5 mm prolongato et ventraliter bilobulato. Ovarium 4-loculare apice modice setoso. Semina ca. 0.5 mm longa. Chromosomatis numerus: $n = 11$.

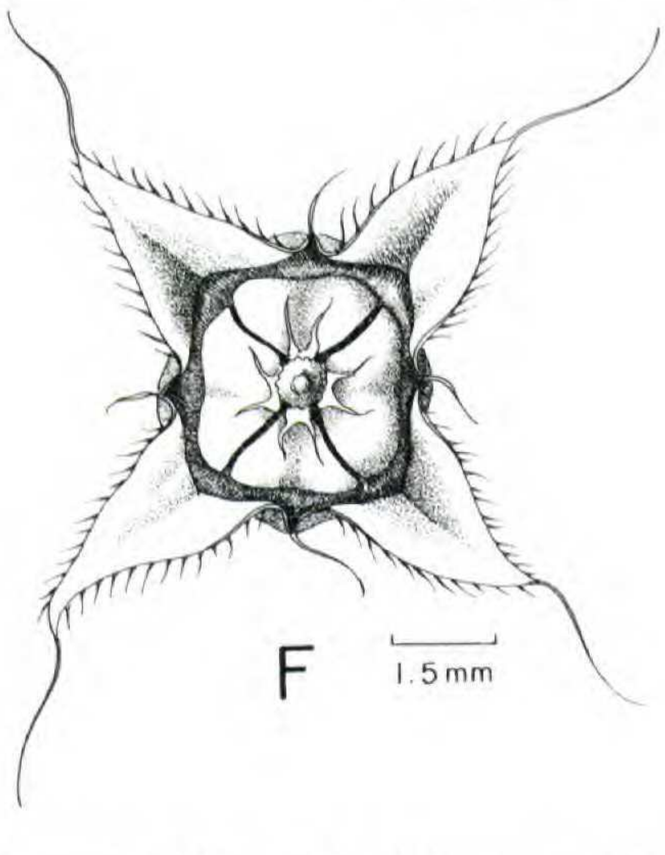
Prostrate matting herb commonly rooting at nodes with trailing branches to 5 dm long. Cauline internodes quadrate to rounded-quadrate, sparsely to moderately covered with ascending or incurved, minutely barbellate multicellular trichomes on stem angles but sparingly pubescent to glabrate between the angles. Mature leaves equal to somewhat unequal in size in each pair; petioles 2–7 mm long, 0.5 mm wide; blades chartaceous when dry, entire











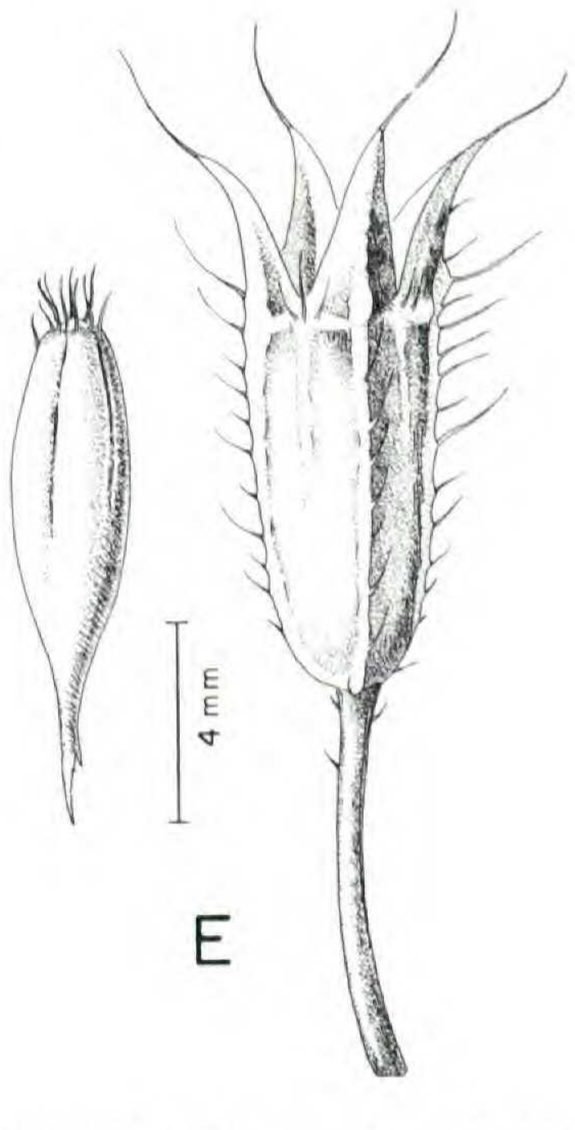


Figure 2. *Pilocosta nubicola* Almeda. —A. Habit. —B. Representative leaves, abaxial surface (left) and adaxial surface (right). —C. Ventral view of antepetalous stamen (left) and lateral view of antesepalous stamen (right). —D. Petal. —E. Ovary at anthesis (left) and mature hypanthium (right). —F. Capsule and enveloping quadrate hypanthium as seen from above. —G. Seeds. (A–F from the holotype; G from *Dryer 1059*, CAS.)

but fringed with coarse trichomes (0.5–1 mm long) closely appressed to blade margin, 12–26 mm long, 8–18 mm wide, ovate to elliptic-ovate, 5–7-plinerved, innermost pair of primary veins diverging from midvein 1.5–4 mm above base of blade, apex acute, base obtuse to rounded; adaxial surface moderately to densely villous; abaxial surface sparsely to moderately strigose on and between elevated primary veins. Flowers solitary, axillary, and ebracteate on sparsely pubescent pedicels 5–9(–12) mm

long. Fruiting hypanthium free from ovary but fully enveloping it, 7–8 mm long to the torus, 2.5 mm wide on each flat side, subcylindric, conspicuously quadrangular, moderately to sparsely beset with appressed, incurved or antrorsely spreading barbellate trichomes along the torus abaxially and on the four prominent angles but glabrous between them. Calyx lobes (fruiting hypanthia) lance-triangular, ciliate and tipped with an apical trichome 1.5–2.5 mm long, glabrous adaxially, sparsely beset with antrorsely spreading trichomes mostly on the midvein abaxially, 3 mm long and 2 mm wide at the base. Petals 4, pink but white basally on the adaxial surface, obovate, entire, ciliate, 12.5–15 mm long, 10–13.5 mm wide. Stamens 8, alike in form but unequal in size, thecae curved upward, yellow, linear-subulate with a ventrally inclined apical pore, channeled along the connective, which is prolonged basally and modified into a bilobate ventral appendage. Larger (antesepalous) stamens: filaments 3.5–4 mm long, anthers 4 mm long, 0.5 mm wide, connective prolongation and appendage each 0.25 mm long. Smaller (antepetalous) stamens: filaments 3–3.5 mm long, anthers 2.5 mm long, 0.5 mm wide, connective and appendage each just under 0.5 mm long. Ovary superior, 4-celled, glabrous but setose apically around the stylar scar. Style 7–8 mm long, glabrous, declinate and curved apically below the punctiform stigma but often appearing straight when dry. Capsule dry, semiwoody, loculicidal; seeds ca. 0.5 mm long, cochleate and tuberculate, dark brownish black at maturity. Chromosome number: $n = 11$.

Distribution. Known only from the Monteverde Cloud Forest Reserve on the Cordillera de Tilarán in northwestern Costa Rica where it typically grows in exposed areas bordering cloud forests or along trails with an Atlantic slope exposure at elevations of 1,200–1,580 m. This species was listed as *P. aff. erythrophylla* in the vascular plant checklist of the Monteverde Cloud Forest Reserve (Haber, 1991).

Like *Pilocosta erythrophylla*, one of the most conspicuous features of *P. nubicola* is the deep red pigmentation of hypanthia and abaxial foliar surfaces. These two species also share an herbaceous habit, stamens that are completely yellow in color, and hypanthia that are pubescent on the four angles but glabrous between them. It is the similarity in these characters that weighed heavily in the initial decision to associate *P. nubicola* with *P. erythrophylla* (Almeda & Whiffin, 1981).

The most consistent differences between *Pilocosta nubicola* and *P. erythrophylla* involve the size, venation, and pubescence of the leaves. In the former, leaf blades are 12–26 × 8–18 mm, 5–7-plinerved with the innermost pair of primary veins diverging from the midvein 1.5–4 mm above the blade base, and abaxial pubescence that is sparsely to moderately strigose on and between the elevated primary veins. In *P. erythrophylla* leaf blades are 2–13 × 1–9 mm, 3–5-nerved, or if plinerved, the innermost pair of primaries diverge from the midvein 0.5–1 mm above the blade base, and are essentially glabrous abaxially or with scattered trichomes restricted to the elevated primaries.

Aside from differences in base chromosome numbers for each species ($n = 11$ in *P. nubicola* vs. $n = 7$ in *P. erythrophylla*) other diagnostic differences between them are mostly quantitative. In *P. nubicola*, the petals are consistently larger (12.5–15 × 10–13.5 mm) and the pollen has a mean diameter of 20.3 μm (range 18.8–23.5 μm). In contrast, *P. erythrophylla* has petals that are 7–11 × 5–9 mm and a consistent mean pollen diameter of 15.9 μm for both diploid (range 15.3–16.5 μm) and tetraploid (range 14.1–16.5 μm) populations.

The only other species with which *Pilocosta nubicola* might be confused is *P. nana*. These species are similar in habit, leaf size, and coloration of the anther thecae but are readily distinguished by the features described in the key.

The name for this species is derived from *nubicolus*, Latin for dwelling among the clouds, in reference to the Monteverde Cloud Forest Reserve where *P. nubicola* is apparently endemic.

Paratypes. COSTA RICA. **Alajuela–Guanacaste–Puntarenas Border:** Cordillera de Tilarán, Monteverde Cloud Forest Reserve on road beyond Sendero Pantanoso jct. enroute to Peñas Blancas Valley, 23 Feb. 1986 (fl), *Almeda et al. 5072* (CAS, CR, TEX); El Brillante, Monteverde, Cordillera de Tilarán, 14 Dec. 1976 (fl, fr), *Dryer 1059* (CAS, F). **Puntarenas:** 4 km E of Monteverde, Cordillera de Tilarán, 19 May 1977 (fl), *Lawton 1169* (F).

5. Pilocosta oerstedii (Triana) Almeda & Whiffin, Syst. Bot. 5: 305. 1980 [1981]. *Pterolepis oerstedii* Triana, Trans. Linn. Soc. London 28: 40. 1871. TYPE: Costa Rica, without further locality, *Oersted 2967* (lectotype, designated by Almeda & Whiffin (1981), BM; isolectotypes, C, CAS, F, US).

A distinctive field character of *P. oerstedii* is the striking silver silky indument on adaxial foliar surfaces.

This species is local and uncommon throughout most of its range. Available collections exhibit a patchy distribution in central Costa Rica from the San Ramon region and the Cerros de Escazú to the

northwestern sector of the Cordillera de Talamanca with disjunct populations in the western provinces of Panama (Bocas del Toro and Chiriquí) at 900–2,000 m. The few recent collections of *P. oerstedii* were made in the Cerro Colorado region of western Panama, the only area to my knowledge where the species is represented by more than just a few individuals.

Pilocosta oerstedii is fairly uniform morphologically but puzzling in having haploid chromosome numbers of $n = 11$ (Panama) and $n = 18$ (Costa Rica). Additional sampling is needed to determine whether there is a consistent geographic pattern to these disparate chromosome numbers.

Solt & Wurdack (1980) reported a chromosome count of $2n = 66$ for this species [as *Tibouchina oerstedii* (Triana) Cogniaux]. Examination of the voucher (*Schnell 1027*, US) reveals that it is in fact *P. nana*, the only species in the genus with hexaploid populations.

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